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Butterfly diversity loss in Flanders (north Belgium): Europe's worst case scenario?

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Abstract

We illustrate the strong decrease in the number of butterfly species in Flanders (north Belgium) in the 20th century using data from a national butterfly mapping scheme. Nineteen of the 64 indigenous species went extinct and half of the remaining species are threatened at present. Flanders is shown to be the region with the highest number of extinct butterflies in Europe. More intensive agriculture practices and expansion of house and road building increased the extinction rate more than eightfold in the second half of the 20th century. The number of hot spots decreased considerably and the present-day hot spots are almost exclusively in the northeast of Flanders. Species with low dispersal capacities and species from oligotrophic habitats decreased significantly more than mobile species or species from eutrophic habitats. We discuss these results in a northwest European context and focus on concrete measures to preserve threatened butterfly populations in Flanders.

Keywords: Butterflies; Biodiversity; Hot spots; Conservation; Flanders

1. Introduction

In contrast with many other invertebrates, butterflies have been studied and extensively collected by amateur entomologists and scientists in the past. Particularly in Europe, catalogues on the occurrence of different species have been published since the beginning of the 19th century (e.g. De Selys-Longchamps, 1837, for Belgium). Ever since, interest in butterflies has only increased and they are among the best-known groups and one of the most frequent conservation targets amongst invertebrates (New, 1997). Many butterfly species have high demands for habitat quality (including microclimate, vegetation structure, co-occurrence of vegetation types at a local scale — Thomas, 1994) and they often respond quickly to habitat deterioration (e.g. 3 to 30 times faster than their host plants — Woiwod and Thomas, 1993). They are, therefore, generally considered to be useful indicators of habitat quality changes in particular terrestrial habitats (e.g. grasslands; Erhardt and Thomas, 1991) and have some potential to be an effective 'umbrella group' for biodiversity conservation (New, 1997), although no single species or taxonomic group can be regarded as a universal bio-indicator (Simberloff, 1998). Nevertheless, the availability of distribution data since more than a century, and their specific relations with aspects of habitat quality, make butterflies a relevant group for analysing faunal changes in relation to changes in land-use.

In this paper, we analyse changes in butterfly diversity during the 20th century (and particularly during recent decades) in Flanders, the northern region of Belgium. This northwest European region is characterised by very high human population density and a high mean standard of living, resulting in high pressure on the environment (OECD, 1998). Natural habitats became human-dominated habitats several centuries ago. Although many different faunal elements went extinct during this process (e.g. large herbivores and large mammal predators, but probably also more inconspicuous organisms), many others were able to survive successfully in the traditionally-managed, semi-natural habitats such as dry and wet heathlands, hayfields or coppiced woodlands. Several butterfly species and other thermophilous insects with relatively short-generation

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times (e.g. carabid beetles, grasshoppers) even became dependent on these early successional habitat types for their survival (Thomas, 1993). Since about 1950, land-use progressively became more intensive (industry, agriculture, road and house building) and affected the landscape to a much greater extent. As a result, most traditionally-managed habitats were lost and present-day remnants are small and highly fragmented. Compared to other European countries or regions, nature reserves in north Belgium are very small: only 30 are larger than 100 ha and all reserves together occupy only 1.1% of the total area of Flanders (Decleer and De Belder, 1999). In the countryside the traditional landscape matrix (with small-scaled managed meadows, extended hedgerows, woodlands and large heathlands), is largely replaced by intensively used arable fields and sown grasslands (agro-industry). From the 1960s, this process was accelerated by large agricultural land consolidation projects. Furthermore, there has been a diffuse spread of house building and an expansion of industrial zones (Table 1).

It is expected that such dramatic changes in land-use have a severe impact on the butterfly fauna (among other components of biodiversity) in Flanders. Here, we deal with changes in species numbers, changes in the extent of distribution and changes in hot spots with respect to (Red list) species richness. Since species differ in mobility and habitat use, and hence in their ability to survive in a changing and highly fragmented landscape, patterns are likely to differ among species. Turin and den Boer (1988) have shown that carabid beetles with poor dispersal abilities have declined more than those with good dispersal capacities. We may expect a similar pattern for butterflies with sedentary species showing stronger decreases in distribution area than the more mobile ones. Furthermore, the increased use of fertilisers since the 1950s and the over-production of manure by an oversized stock of cattle (1.7 million — Lauwers et al., 1996) and pigs (6.8 million — Lauwers et al., 1996) have probably led to a stronger decrease in distribution area for species that are confined to oligotrophic habitats (e.g. nutrient poor grasslands and hayfields or heathlands) compared to species that thrive in eutrophic biotopes (e.g. abandoned meadows; van Swaay, 1990; León-Cortés et al., 1999; Van Es et al., 1999). We therefore also examine how changes in distribution relate to mobility and to the habitat type of butterflies in Flanders.

To quantify and analyse changes in butterfly diversity, we used an extensive data set on the former and present-day distribution of the 64 indigenous species that was initially compiled for a documented distribution atlas (Maes and Van Dyck, 1999). Despite their great value and potential use for nature conservation, such distribution data inevitably carry several biases (e.g. temporal and spatial differences in recording effort) causing typical difficulties for the analyses (Dennis and Hardy, 1999; Dennis et al., 1999; Dennis and Thomas, 2000). To reduce such effects maximally, a sub-data set fulfilling several criteria regarding recording intensity was used, rather than the entire data set.

2. Methods

2.1. Study area

Flanders (total area 1 351 200 ha) is the northern, Dutch speaking part of Belgium. It exhibits the typical features of a western industrialised region: extensive industry, infrastructure, house building and agriculture, and a human population density of 431 citizens/km^2 (Van Hecke and Dickens, 1994). The general landscape and topography differ considerably between Flanders and the southern parts of Belgium (Wallonia). Moreover, nature conservation policy is the responsibility of the regional governments rather than the Belgian federal government. Therefore, data from Wallonia were not incorporated. A survey of the butterflies of Wallonia, including a Red List, is given by Goffart et al. (1992); Van Swaay and Warren (1999) give the threat status of all indigenous butterflies in Belgium.

Table 1
Change of land use (in ha) in Flanders between 1834 and 1995[a]

Land use	1834	1980	1995 (%change)
Built-on areas	11,670	135,120	202,239 (+1633%)
Other open space (e.g. dumping grounds, airfields, mine waste heaps...)	4130	31,605	35,686 (+764%)
Gardens, parks and recreation zones	3553	28,080	24,960 (+603%)
Roads, rivers and canals	44,985	93,046	106,745 (+137%)
Agricultural grasslands	169,230	311,670	296,815 (+75%)
Woodland	142,490	111,590	108, 795 (−24%)
Arable land, horticulture, orchards	808,640	589,030	529,184 (−34%)
Heathlands and waste lands (=nutrient poor grasslands)	163,359	52,151	47,972 (−71%)

[a] The figures for 1834 and 1980 are based on Van Der Haegen (1982), the figures for 1995 are based on Ministerie van de Vlaamse Gemeenschap (1996). Between brackets the relative change (in percentage) between the area occupied in 1834 and that in 1995.

2.2. Origin of the data

For the Flemish butterfly atlas, about 190 000 records were collected on all butterfly species observed in Flanders since 1830 (Maes and Van Dyck, 1999). This extensive mapping scheme was co-ordinated by the Flemish Butterfly Working Group. Data came from: (1) collections of scientific institutions and private collectors (±10 000 records), (2) reports in national and local journals (±5000 records) and (3) field observations (±175 000 records). Field observations were made by about 600 volunteers. Data from collections and from literature reports mainly dated from 1901–1980 while the field observations were mainly from 1985–2000. For all records at least the species, the year of observation and the exact location were noted. For all locations at least the 5×5 km Universal Transverse Mercator (UTM) square code was recorded and if possible even the 1×1 km UTM square code. These 5×5 km squares ($n = 644$) were used as units of distribution. In our study we used the year 1991 as pivotal date because this coincides with the start of the large-scale butterfly mapping project. A recent pivotal date reflects the current situation without possible time lags (species that have gone extinct in the meantime). Fig. 1 gives an overview of the pre- and post-1991 coverage of the mapping scheme with numerical values for species richness per square and Fig. 2 shows the number of records per 5-year period in the 20th century.

2.3. Changes in species numbers and in diversity and Red List species hot spots

To determine changes in species numbers, we counted the number of indigenous species per five-year period during the 20th century. This enabled us to calculate an extinction rate for butterflies (Thomas and Morris, 1994) and to compare the present species richness with the historical one.

We determined present and historical species rich areas ('hot spots') by counting the number of species per square before and after 1991. Both the total number of species per square (i.e. diversity hot spots, DHS) and the number of Red List species per square (i.e. Red List species hot spots, RLHS) were analysed. Each species was assigned a Red List status according to Maes and Van Dyck (1999; Appendix). Red List categories are those proposed by the IUCN Species Survival Commission

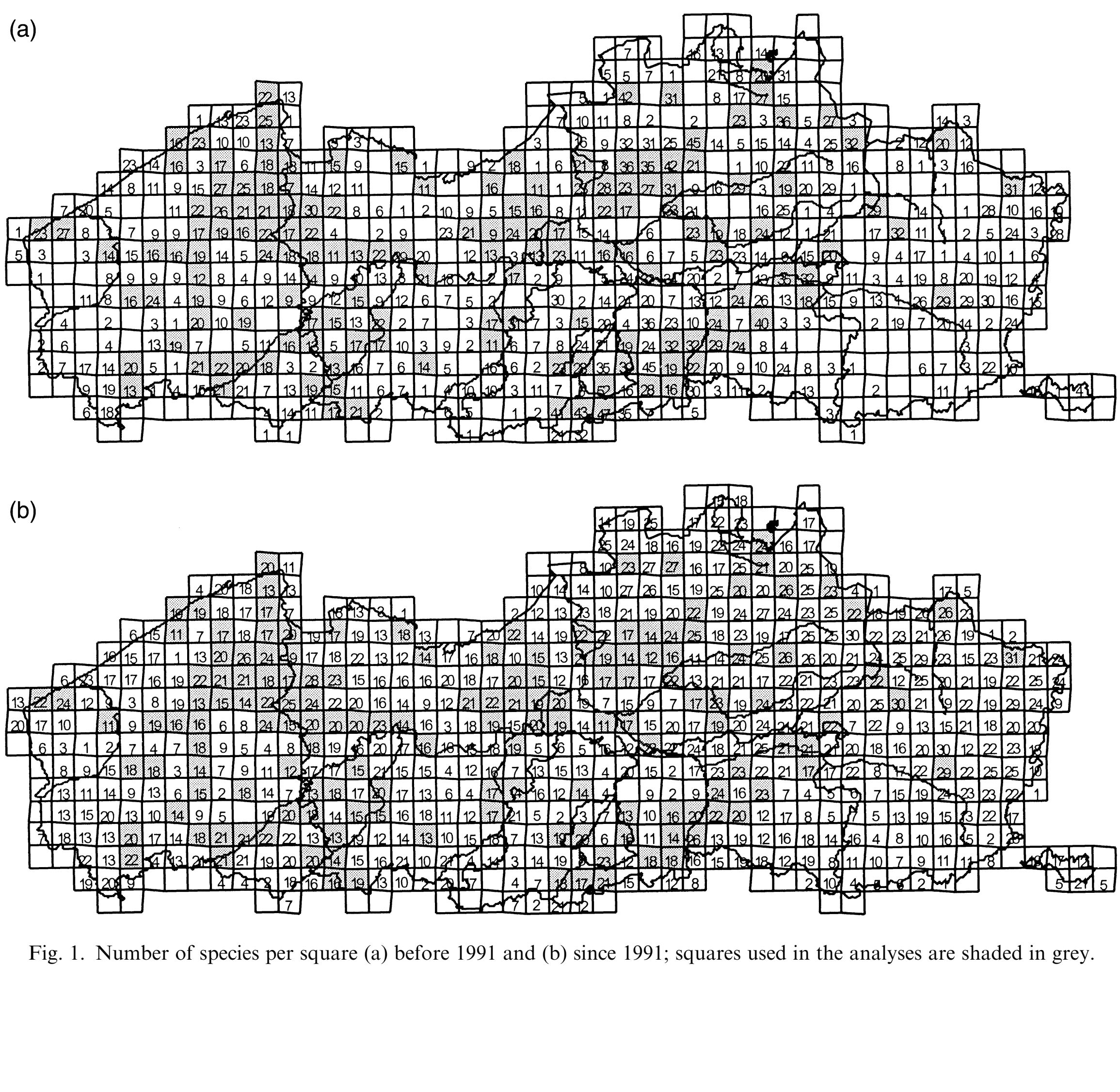

Fig. 1. Number of species per square (a) before 1991 and (b) since 1991; squares used in the analyses are shaded in grey.

(1994), adapted to Flanders (Maes et al., 1995; Maes and van Swaay, 1997). DHS and RLHS are arbitrarily defined as the top 5% of the recorded squares, ranked by decreasing number of all species and of Red List species respectively, in the period after 1991 (Prendergast et al., 1993). DHS in Flanders are determined as squares with ⩾26 species and RLHS as squares with ⩾five Red List species. To estimate changes in the number of DHS and RLHS between the two periods, we used criteria similar to Prendergast and Eversham (1995): hot spots are determined using the present-day data, and changes in the numbers of hot spots are relative to the recent period (i.e. since 1991).

2.4. Changes in distribution area

To analyse changes in distribution area, we compared the number of squares in which each species was recorded before and after 1991. However, because the data originate from different sources (collections, literature citations and field observations) and were collected on a voluntary basis, there is a bias in sampling effort both in time, space and targeted species (Dennis and Hardy, 1999; Dennis et al., 1999; Dennis and Thomas, 2000). We therefore restricted the analyses to squares we considered sufficiently well investigated in both periods. To select these squares, we counted the number of UTM squares in which each species was mapped during both periods and ranked them in decreasing number of squares. For both periods the top six consisted of the same species (although in a different order), i.e. *Pieris brassicae*, *Pieris rapae*, *Pieris napi*, *Inachis io*, *Aglais urticae* and *Pararge aegeria*. We restricted the analysis to those squares in which all these six species were recorded in both periods. This criterion restricted the analysis to 150 squares (23% of all squares). Seven species were excluded from the analysis because they reach the margin of their distribution area in Flanders (according to Tolman, 1997, and Bink, 1992; Appendix). This reduced the number of species analysed to 57 of the 64 indigenous species. The 150 squares used in this analysis are fairly well spread over the geographical regions of Flanders (Dufrêne and Legendre, 1991): 33 squares are situated in the Loamy region (17% of all squares in this region), 34 squares in the Campine region (17% of all the squares in this region), 13 squares in the Coastal region (19% of all the squares in this region) and 70 squares in the Sandy-loamy region (37% of all the squares in this region). Therefore, we consider the 150 squares used for the analyses as representative of Flanders. Furthermore, the number of records is comparable in both periods: 12 393 records (i.e. a species in a square in a given year) date from before 1991 and 10 035 records date from since 1991.

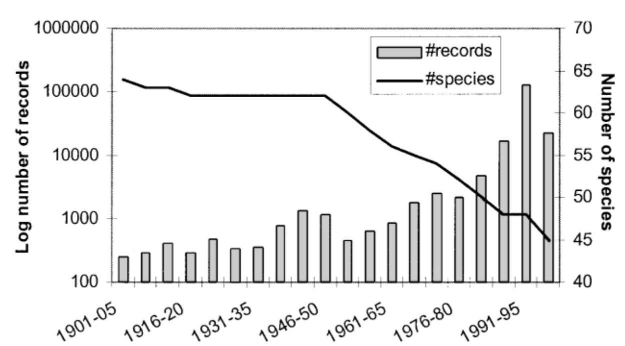

Fig. 2. Number of records (left *y*-axis, log scale) and number of species (right *y*-axis) per 5-year period in Flanders in the 20th century.

2.5. Changes in distribution area in relation to mobility and habitat type

To analyse relationships between changes in distribution area on the one hand, and dispersal capacity and habitat type on the other hand, all indigenous species were assigned to a mobility class and to a nutritional value of the breeding habitat (Appendix). Mobility for each species was derived using Bink's (1992) method of nine mobility classes, ranging from very sedentary to wanderers. To avoid small sample sizes, the number of classes was reduced to four (1 = very sedentary, 2 = sedentary, 3 = fairly sedentary, 4 = mobile–very mobile) by lumping the first and second on the one hand, and the fifth, sixth and seventh mobility classes on the other hand; the eight and ninth mobility class refer to vagrants that are not indigenous in Flanders (e.g. *Vanessa cardui*). For the nutritional value of the breeding habitat, the classification is based on the average nutrient number (Stickstoffzahl, Ellenberg et al., 1992) of the hostplant(s) (Oostermeijer and van Swaay, 1998) and additional ecological literature (e.g. Emmet and Heath, 1989; Tax, 1989; Bink, 1992). We distinguished three nutritional values of the breeding habitat: (1) oligotrophic; (2) mesotrophic; and (3) eutrophic. To avoid a tendency towards no change in distribution area of the most common species, the six species used to determine the sub-set of squares (*Pieris brassicae*, *P. rapae*, *P. napi*, *Inachis io*, *Aglais urticae* and *Pararge aegeria*) were excluded from this analysis. This reduced the number of species analysed from 57 (see above) to 51.

2.6. Statistical analysis

The complete data set was used to determine changes in species numbers and for the hot spot analysis. Changes in distribution area in relation to mobility and to nutritional value of the breeding habitat were analysed with the sub-data set as described above. The changes in distribution area were defined as "Log_{10} (number of squares since 1991 + 1)–Log_{10} (number of squares before 1991 + 1)" (Appendix). Effects of mobility and

nutritional value of the breeding habitat on changes in distribution area were tested separately by one-way analysis of variance since mobility and breeding habitat were not statistically independent (Sokal and Rohlf, 1988).

3. Results

3.1. Butterfly diversity and Red List species

Butterfly diversity decreased strongly during the 20th century: 44 species show a negative trend (of which 21 declined significantly, χ^2-test: $P < 0.05$), while only 13 species show a positive trend (of which four increased significantly, χ^2-test: $P < 0.05$). Seven species show no trend: the six species used to determine the restricted data set and *Heteropterus morpheus*, a very rare species restricted to one grid square. The number of species that decreased or increased significantly and remained stable differs highly significant from what can be expected under the null-hypothesis of no changes ($\chi^2 = 28.7$, $P < 0.001$). Of the 35 species that were considered very rare to fairly common before 1991 (present in 1–50 squares, i.e. 1/3 of the total number of squares in the sub-data set), all but three (*Thymelicus sylvestris*, *Aricia agestis* and *Melanargia galathea*) decreased in distribution area. On the other hand, 11 of the 16 species that were common to very common before 1991 (present in 51–150 squares) increased in distribution area; two significant exceptions were *Coenonympha pamphilus* and *Lasiommata megera*.

The number of species per 5-year period decreased since the beginning of the century from 64 in 1901–1905 to 45 in 1996–2000 (Fig. 2). This is an average extinction rate (Thomas and Morris, 1994) of 0.95 species per 5 year period during the 20th century. However, if we compare the first and second half of the century (1901–1950 vs. 1951–2000), the extinction rate was 0.20 species/5 year period and 1.70 species/5 year period respectively which means that it increased more than eightfold during the second half of the 20th century.

3.2. Diversity hot spots (DHSs) and Red list hot spots (RLHSs)

In the period before 1991, 57 squares were determined as DHSs of which 51 fell below the threshold of 26 species in the period after 1991. Only six squares preserved their status as DHS. In the period after 1991, 16 squares were gained as DHS compared to the period before 1991 (Fig. 3a).

In the period before 1991, 107 squares were determined as RLHSs of which 96 fell below the threshold of five Red List species in the period after 1991. Only 11 preserved their status as RLHS. In the period after 1991, 14 squares were gained as RLHS compared to the period before 1991 (Fig. 3b). A higher (spatial) recording intensity in the second period is most likely responsible for the 'gained' DHS and RLHS (Table 2) and not the colonisation of new squares by (Red List) species. The average number of (Red List) species and records in the former and present DHS and RLHS is given in Table 2.

Hot spots (both DHS and RLHS) are mainly lost around Brussels in the south, around Antwerp in the north and in the dune area (Fig. 3a, b). With very few exceptions, the present-day hot spots are situated on the sandy soils in NE-Flanders (Campine region) where heathlands, nutrient poor grasslands and woodlands still co-occur.

3.3. Changes in distribution area in relation to mobility and habitat type

Changes in distribution area differed significantly with level of mobility and with nutritional value of the breeding habitat. Butterfly species with a low dispersal capacity experienced a more severe loss in distribution area than species with a higher dispersal capacity: Kruskal–Wallis analysis of variance (ANOVA): H (3, $n = 51) = 10.187$, $P = 0.017$ (Fig. 4a). Species of oligotrophic habitats experienced a more severe loss in distribution area than did species of mesotrophic and eutrophic habitats: Kruskal–Wallis ANOVA: H (2, $n = 51) = 15.781$, $P < 0.001$ (Fig. 4b). A posteriori tests for differences in changes in distribution area among mobility classes and among nutrient values of the breeding habitat are given in Fig. 4.

4. Discussion

4.1. Biases in comparing historical and recent data

Establishing the conservation status and distribution trends of species — and hence of at least parts of the biodiversity — for a political relevant unit (region or country), has been a traditional and valuable tool to evaluate the efficiency of nature conservation efforts. However, when comparing former and present-day distribution data, biases in time, space and targeted species (rare vs. common species) can hardly ever be excluded due to differences in collection methods and time periods considered (Dennis et al., 1999; Dennis and Thomas, 2000). Restricting the comparison to records from butterfly collections was not possible since hardly any collection data are available for the recent time period (since 1991). We have attempted to maximally reduce the biases in the data set by using a limited set of well investigated squares during the two time periods. Other criteria to obtain subsets of well investigated squares (e.g. at least 15 species present/square, at least 75% of

the very common species present/square) or a different pivotal date (e.g. 1980, 1970 or even 1950), yielded very similar results as the ones described in this paper, and do not change the main conclusion that Flanders is one of the regions with the severest butterfly loss in Europe. Bias is mainly due to the undermapping of most common species in the earlier periods compared to recent butterfly mapping schemes. Rare species however, were fairly well mapped both before and after 1991. Before 1991 rare species were actively looked for, and are therefore, well represented in collections and in literature citations; after 1991 the Flemish butterfly mapping scheme placed an emphasis on detailed mapping of the distribution of Red List species on topographic maps. Declining trends of rare species are, although severe for most of them, probably still underestimated since they are based on relatively coarse-grained distribution data (Thomas and Abery, 1995) and since not all past populations were mapped before they went extinct, whereas almost all recent populations of rare butterflies are known. On the basis of UTM squares most common species seem to have a stable or even an increasing distribution, but at the population level, these species may show an equally strong decrease as some of the rare

Table 2
Average number of species in the lost, maintained and gained diversity hot spots (DHS) before and since 1991 and average number of Red List species in the lost, maintained and gained Red List hot spots (RLHS) before and since 1991[a]

	DHS		RLHS	
	< 1991	⩾1991	< 1991	⩾1991
Lost hot spots	32.94 (5.8)	18.71 (72.7)	9.88 (4.9)	1.97 (61.4)
Maintained hot spots	31.50 (13.0)	28.50 (187.1)	9.00 (9.1)	6.18 (141.9)
Gained hot spots	14.57 (10.1)	27.19 (150.0)	1.64 (8.8)	5.79 (111.0)

[a] The average number of records per square per 5 year period in lost, maintained and gained hot spots before and since 1991 are in parentheses.

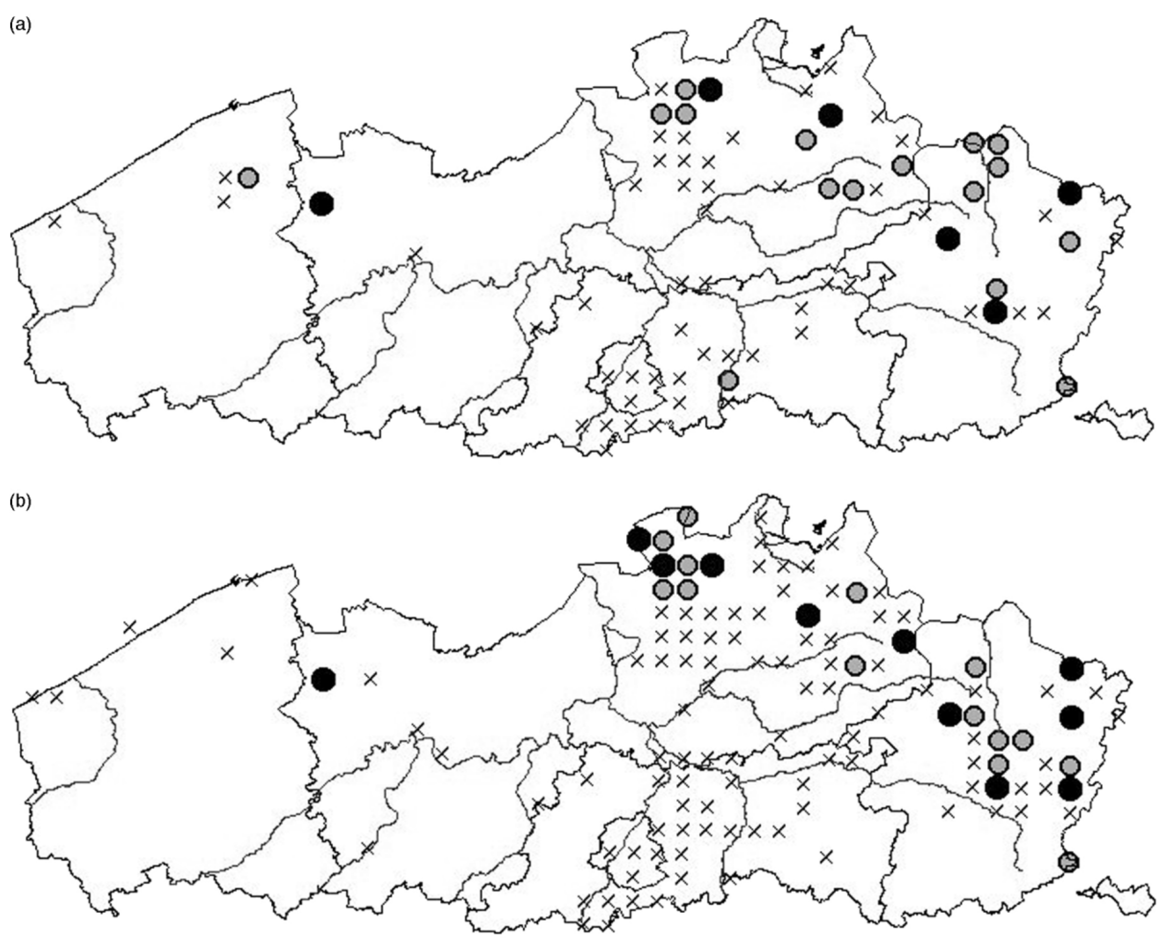

Fig. 3. Lost (crosses), maintained (grey dots) and gained (black dots) (a) diversity hot spots and (b) Red List species hot spots in Flanders.

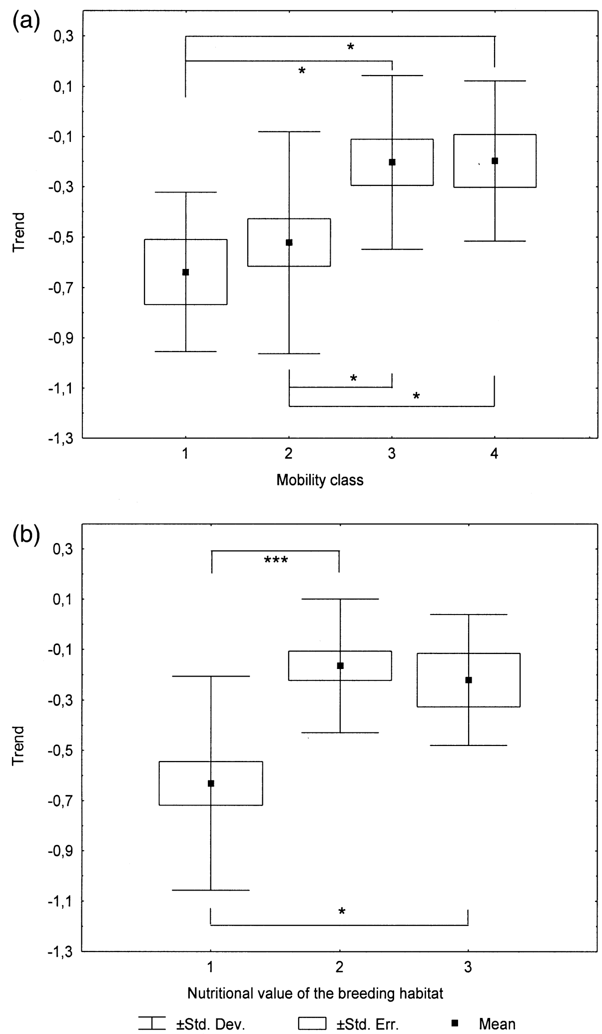

Fig. 4. Mean trend, standard error and standard deviation (a) per mobility class and (b) nutritional value of the breeding habitat. Number of species per mobility class (MC) is: MC 1 ($n=6$), MC 2 ($n=22$), MC 3 ($n=14$), MC 4 ($n=9$). Number of species per nutrient value of the breeding habitat (NV) is: NV 1 ($n=24$), NV 2 ($n=21$), NV 3 ($n=6$). A posteriori tests (Least significant difference test) for differences in changes in distribution area (a) among mobility classes and (b) among nutrient values of the breeding habitat are indicated by lines between classes (only significant differences are shown): *, $P<0.05$; ***, $P<0.001$.

species (Cowley et al., 1999; León-Cortés et al., 1999, 2000). Declining relative abundances of still widely distributed butterfly species (e.g. *Inachio io*, *Aglais urticae*) have been noticed from butterfly transect counts in the 1990s in Flanders and The Netherlands (van Swaay et al., 1997; van Swaay and Ketelaar, 2000).

4.2. Butterfly diversity loss

In Flanders 30% of the indigenous butterfly species went extinct during the 20th century and half of the remaining species is threatened (Maes and Van Dyck, 1999). Furthermore, about 90% of the former hot spots (both diversity and Red List species hot spots) have been lost despite a strong increase in recording intensity (Table 2 and Fig. 2). The strong deterioration of the butterfly fauna is not restricted to Flanders, but also affects most other northwest European countries or regions: the Netherlands (Wynhoff and van Swaay, 1995), Wallonia (S-Belgium) (Goffart, 1997), Baden-Württemberg (Ebert and Rennwald, 1993) and Germany (Pretscher et al., 1998); Table 3). Denmark (van Swaay and Warren, 1999) and Great Britain (Warren et al., 1997) are the only two northwest European countries with a relatively limited number of extinct and threatened species. Within Flanders, butterflies also show the highest number of extinct and Red List species compared to other taxonomic groups for which the conservation statuses are known (Table 4).

The decline in the number of hot spots and the regions where they were lost are largely coincident for overall species richness and Red List species richness. For instance, the larger woodlands around Brussels (e.g. the Walenboscomplex — Tips, 1977) used to hold many butterfly species typical of open woodland, grasslands, and even heathlands on sandy areas in the woodlands. Almost all these butterfly species have disappeared from these situations because of, either economic exploitation of the woodlands, or a lack of appropriate conservation management. In the dune area, the strong expansion of house building for tourism considerably reduced the area of semi-natural grasslands; ceasing of grazing in several

Table 3
Comparison of the number of extinct and Red List species between some NW-European countries or regions[a]

Country or region	Extinct	Red List	%E+RL	Total number
Flanders (Maes and Van Dyck, 1999)	19 (30%)	22 (34%)	64	64
The Netherlands (Wynhoff and van Swaay, 1995)	17 (24%)	28 (40%)	64	70
Wallonia (Goffart, 1997)	15 (14%)	50 (48%)	63	104
Baden-Württemberg (Ebert and Rennwald, 1993)	4 (3%)	80 (58%)	61	137
Germany (Pretscher et al., 1998)	6 (3%)	87 (47%)	50	185
Denmark (van Swaay and Warren, 1999)	4 (6%)	18 (26%)	35	68
Great-Britain (Warren et al., 1997)	4 (7%)	8 (14%)	20	59

[a] The countries or regions are ordered in decreasing percentage of Extinct and Red List (%E+RL) species.

remnants (Vermeersch, 1986) further reduced the availability of early-successional habitats for several Red List species. In northeast Flanders, the majority of heathlands and nutrient-poor grasslands were transformed into arable land, conifer plantations or other land-uses, although some small to medium-sized heathlands and deciduous woodlands still remain, often in military areas.

The extinction rate of butterfly species in Flanders has increased markedly compared to the first part of the 20th century, despite an increasing total number of data since 1950 (Fig. 2). Several factors that contributed to this decline are still operating. Indeed, the Flemish government has recently received a European Commission's letter giving formal notice (i.e. the first step in the procedure towards a conviction) for insufficient efforts to reach the minimal standards regarding nitrogen pollution due to the over-production of manure (EU Nitrogen Directive) and one regarding the completion of the habitat network NATURA 2000 (EU Habitat Directive). Assuming a linear extinction rate of 1.70 species/5 year (as in the second half of the 20th century), Flanders will lose the 22 remaining Red List species in a period of only 65 years.

As in most other northwest European countries, destruction of suitable butterfly habitats, habitat fragmentation and declining habitat quality are the factors responsible for the deterioration of the butterfly fauna (Thomas, 1984, 1991; van Swaay, 1990; Goffart et al., 1992; Warren et al., 1997; Maes and Van Dyck, 1999). In Belgium and in the Netherlands in general and in Flanders in particular, the increase in built-on area and the intensification and expansion of agriculture (Table 1) destroyed, or decreased the quality of, many suitable butterfly habitats. Species have disappeared even within nature reserves or other protected areas and still are disappearing due to inappropriate management (Thomas, 1984; van Swaay, 1990; Warren, 1993). Nature management has often been focused on plants and particularly birds which is not necessarily suitable for butterflies and other invertebrates (Thomas, 1994). Two recent cases illustrate how inappropriate management caused great damage and even the extinction of highly threatened butterfly populations. In a Flemish nature reserve overgrazing of the host plant *Gentiana pneumonanthe* lead to the local extinction of *Maculinea alcon*, while in the Netherlands, a wrong mowing date severely reduced the number of individuals in the reintroduced populations of *Maculinea teleius* (Wynhoff, 1998).

Of the species with the strongest decline in distribution area, all but two used to be relatively rare in the past, while of the species that increased their distribution area all but two were already widespread in the past. A similar pattern has been shown for butterflies in the UK (Pollard and Yates, 1993) and for amphibians and reptiles in Flanders (Bauwens and Claus, 1996). The extinction of a local population of a rare butterfly is therefore often definitive, while common and more mobile species are able to colonise new sites.

4.3. Changes in distribution area in relation to mobility and habitat type

Species with limited dispersal capacities and species restricted to oligotrophic habitats decreased significantly more strongly than mobile species and than species from eutrophic habitats. The fact that less mobile species decreased more strongly than the more mobile ones seems obvious. Once the habitat of a sedentary species is destroyed, it is unable to find suitable habitat patches that are beyond its dispersal range. Furthermore, the loss of a habitat patch has far greater consequences for a sedentary species in a metapopulation than for a mobile one in an open population: metapopulations of sedentary species fall apart in isolated populations and become more susceptible to

Table 4
Comparison of the number of Red List species between different taxa in Flanders[a]

Taxonomic group	Extinct species	Red List species	%E+RL	Total number
Butterflies (Maes and Van Dyck, 1999)	19 (30%)	22 (34%)	64	64
Dragonflies (De Knijf and Anselin, 1996)	9 (16%)	20 (34%)	50	58
Amphibians/reptiles (Bauwens and Claus, 1996)	2 (11%)	6 (32%)	42	19
Mammals (Criel, 1994)	11 (18%)	13 (22%)	40	60
Empidid flies (Grootaert, in preparation)	31 (13%)	49 (20%)	32	248
Higher plants (Cosyns et al., 1994)	81 (6%)	325 (25%)	32	1288
Breeding birds (Devos and Anselin, in preparation)	4 (3%)	44 (28%)	30	159
Carabid beetles (Desender et al., 1995)	32 (9%)	66 (19%)	28	352
Spiders (Maelfait et al., 1998)	9 (1%)	144 (24%)	25	604
Fish (Vandelannoote and Coeck, 1998)	11 (20%)	2 (4%)	24	55
Dolichopodid flies (Pollet, 2000)	22 (8%)	39 (15%)	23	260

[a] The taxonomic groups are ranked in decreasing percentage of Extinct and Red List species (%E+RL).

extinction (Harrison, 1991; Thomas and Hanski, 1997). At present, habitat patches are destroyed at a much higher speed than the colonisation rate of most species living in a metapopulation structure (e.g. *Melitaea cinxia* is now confined to some canal borders and road verges in the northeast of Flanders).

Species of oligotrophic habitats used to occur in the traditionally managed agricultural landscape. Since agriculture became more intensive in the second half of the 20th century (e.g. artificial fertilisers, increasing numbers of stock on farms, land consolidation projects — Nysten, 1994), many (thermophilous) butterfly species were no longer capable of completing their life cycle due to an increased mowing frequency in intensively used agricultural land or due to taller vegetation, and thus a colder microclimate, in abandoned hayfields (Thomas, 1993). Belgium is one of the countries in Europe with the highest nitrogen input on arable land (17.6 tons/km^2 arable land — OECD, 1998). Furthermore, since agriculture is much more intensive in Flanders than in Wallonia, this figure is probably an underestimate for the northern part of the country. On average, arable land in Flanders has a surplus on the nutrient balance of 236 kg N/ha and of 34 kg P/ha (Vanongeval et al., 1998). The excessive use of nitrogen and phosphorus has direct consequences on the vegetation structure of grasslands and hence on grassland butterflies (Thomas, 1993; Geypens and Rutten, 1994). Indirectly, nutrient deposition and groundwater polluted with nutrients can change the vegetation type and structure in wet heathlands (causing domination of *Molinia caerulea*), in woodlands (causing domination of *Deschampsia flexuosa* and declining tree quality) and in marshes and moist grasslands (Geypens and Rutten, 1994). Most parts of Flanders have a nitrogen deposition of less than 30 kg/ha/year, but in intensive agricultural areas it reaches peaks of more than 50 kg/ha/year (in north Flanders) to even 70 kg/ha/year (in west Flanders; Vanongeval et al., 1998). Examples of species of oligotrophic grasslands showing extreme declines are *Lycaena tityrus* (Fig. 5, see also van Swaay, 1995), *Polyommatus semiargus* and *Melitaea cinxia* in dry habitats and *Boloria selene* in wet habitats. Even fairly common species of dry grassland habitats (e.g. *Lycaena phlaeas*, *Polyommatus icarus*, *Coenonympha pamphilus*, and *Lasiommata megera*) show declining trends that are most probably still underestimated from a census with a coarse grained grid (Cowley et al., 1999; León-Cortes et al., 1999, 2000).

4.4. Butterfly and biodiversity conservation in Flanders

Given the large number of extinct and threatened butterfly species, particularly from habitats with a high conservation value (e.g. dry and wet heathlands, open broad-leaved woodland, flower-rich hay meadows), Flanders urgently needs extra efforts regarding the conservation and restoration of both the quantity and quality of habitat networks. The Flemish government and Ministry of Nature Conservation are well aware of this need and since 1997 a new Decree on Nature Conservation offers much more opportunities and tools to do so. However, the new approaches to realise the Flemish Ecological Network (Decleer et al., 1999) including several new nature development and consolidation projects, are largely site-oriented. Hence, biological realism may be lacking when crucial features of target species (e.g. dispersal) have not been taken into account (e.g. efficiency of corridors, metapopulation structure — Baguette et al., 2000, etc.). Moreover, the

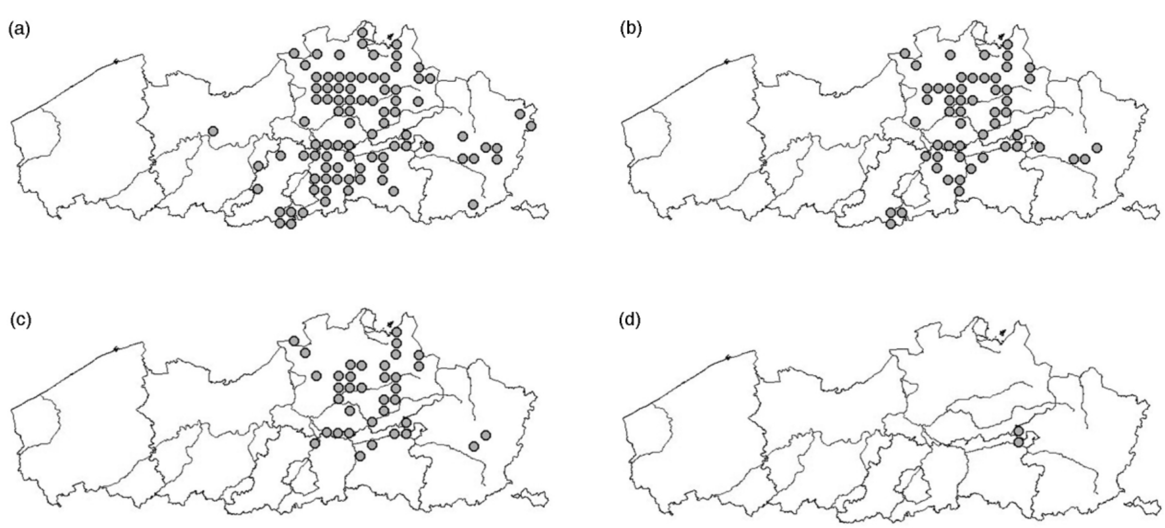

Fig. 5. Distribution of *Lycaena tityrus* in Flanders in the 20th century: (a) 1901–1950, (b) 1951–1970, (c) 1971–1990, and (d) 1991–2000.

general configuration of ecological networks in Flanders will mainly be affected by non-scientific decision rules (e.g. budgets, agreements with other land-users, etc.). Scientific evaluation of different scenarios for the completion of these networks seems crucial in order to maximise the effect of conservation efforts and budgets on the preservation and restoration of biodiversity. Among other taxonomic groups, butterflies may play a valuable role for planning and evaluating site-oriented conservation measures. However, it will be essential to develop a Biodiversity Action Plan for each threatened species.

A large number of populations of threatened species are nowadays restricted to nature reserves or to large military areas. Many of these reserves are too small to contain sustainable populations and undergo strong negative influences from outside the reserve (e.g. nitrogen deposition, recreation from nearby cities, etc.). Priority should be given to the enlargement of existing reserves (including appropriate management — for reviews New, 1991; New et al., 1995; Smallidge and Leopold, 1997) and to the acquisition of non-protected sites with threatened butterflies, especially in the northeast of Flanders where the (Red List) species richness is relatively least impoverished (Fig. 3). The new Flemish Ecological Network is aiming to create an ecological network of: (1) large nature units (total area 125 000 ha); (2) large nature development units (total area 150 000 ha); and (3) ecological corridors. However, populations of some Red List species (*Thecla betulae*, *Satyrium w-album*, *Cupido minimus*, *Aricia agestis*, *Polyommatus semiargus* and *Melitaea cinxia*) are mainly situated outside the preliminary defined networks and need additional protection measures. The completion of ecological corridors is also questionable since no particular species have yet been used as role models. However, little is known about the use of particular corridors or 'stepping stones' by butterflies and other invertebrates and further research on the requirements of corridors is urgently needed (Haddad, 1999; Haddad and Baum, 1999). Nevertheless, a critical screening on the base of best available current knowledge would be highly valuable. For several heathland species large military areas are the strongholds in Flanders (e.g. *Maculinea alcon*, *Plebeius argus*, *Hesperia comma*, *Callophrys rubi* and *Hipparchia semele*). The Flemish Ministry for nature conservation recently signed a protocol with the military authorities that obliges the latter to take into account the presence of threatened species and to draw up specific management plans for military areas.

Legal species protection (in particular, a ban on capturing and collecting) has shown to be a very inadequate measure to ensure their conservation in Flanders (only one, *Maculinea alcon*, of the 13 legally protected species is actually present in Flanders). Furthermore, collecting is only harmful in very small and isolated populations (Thomas, 1983). Hence, a series of species action plans or multi-species action plans (for particular threatened habitats) would be more useful. Presently the first species action plan for an invertebrate is in preparation: i.e. *Maculinea alcon*, a endangered species in Flanders and Belgium (Maes and van Swaay, 1997) and a vulnerable species in Europe (van Swaay and Warren, 1999). Based on national and international relevance, species action plans are desirable for *Pyrgus malvae*, *Hesperia comma*, *Issoria lathonia*, *Boloria selene*, *Melitaea cinxia* and *Coenonympha tullia*. The preservation of existing populations of threatened species remains the first priority; it is only in the second place that reintroduction should be considered (e.g. Ravenscroft, 1992). Potential species for local reintroductions (in order to enforce or recreate a metapopulation structure, cf. Thomas and Jones, 1993) are *Pyrgus malvae*, *Hesperia comma*, *Maculinea alcon*, *Plebeius argus* and *Melitaea cinxia*. Research on the feasibility of national reintroductions of the following species for which potentially suitable habitats are still present in Flanders can be considered: *Maculinea teleius* (extinct since 1980), *Plebeius idas* (extinct since 1984), *Argynnis niobe* (extinct since 1977) and *Euphydryas aurinia* (extinct since 1959). Since several authors have shown that some of the common butterflies are declining as severely as the threatened ones (Cowley et al., 1999; León-Cortés et al., 1999, 2000), additional measures (e.g. education, management advice...) should be taken to preserve the "common" butterflies in the agricultural and rural landscape.

In conclusion, the Flemish butterfly data set is, like most data sets containing historical and recent data, biased in both time and space and in targeted species (rare vs. common species). However, by using a subset of data in which this bias has been reduced maximally, we were able to demonstrate that Flanders is one of the regions with the largest loss in butterfly diversity in Europe. Species with low dispersal abilities and species of oligotrophic habitats suffered most of habitat fragmentation and/or intensification of agriculture. Flanders therefore urgently needs to take actions and adjust current actions to preserve its endangered butterflies and their habitats.

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Appendix

Resident butterflies in Flanders with the number of squares in which the species was observed before and since 1991 in a selection of well mapped squares (for explanation, see text). Species names are according to Karsholt and Razowski (1996)[a]

Species	Before 1991	Since 1991	Trend	RLC	Mobility	Nutritional value
Erynnis tages	11	–	−1.079 (−−−)	Ex	2	1
Pyrgus malvae	23	4	−0.681 (−−−)	En	2	1
Carterocephalus palaemon	19	11	−0.222	Vu	2	2
Thymelicus lineola	99	118	+0.076 (+)	S/LR	3	2
Thymelicus sylvestris	52	59	+0.054	S/LR	2	2
Hesperia comma	19	5	−0.523 (−−)	En	2	1
Ochlodes venata	99	107	+0.033	S/LR	3	2
Papilio machaon	89	97	+0.037	S/LR	4	2
Leptidea sinapis	10	5	−0.263	CE	3	2
Anthocharis cardamines	99	116	+0.068 (+)	S/LR	3	2
Aporia crataegi[(w)]	19	3	−0.699 (−−−)	E	4	2
Pieris brassicae	150	150	0	S/LR	4	3
Pieris rapae	150	150	0	S/LR	4	3
Pieris napi	150	150	0	S/LR	4	3
Gonepteryx rhamni	133	140	+0.022	S/LR	4	2
Lycaena phlaeas	138	128	−0.032	S/LR	3	1
Lycaena tityrus	37	2	−1.103 (−−−)	CE (Ex)	2	1
Thecla betulae	17	11	−0.176	En	2	2
Neozephyrus quercus	44	37	−0.073	S/LR	2	2
Callophrys rubi	27	17	−0.192	Vu	3	1
Satyrium w-album	13	2	−0.669 (−−)	IK	1	3
Satyrium ilicis	29	9	−0.477 (−−)	Vu	2	2
Celastrina argiolus	121	131	+0.034	S/LR	4	2
Maculinea teleius	1	–	−0.301	Ex	1	1
Maculinea alcon	9	4	−0.301	En	1	1
Plebeius argus	29	8	−0.523 (−−−)	Vu	2	1
Plebeius idas	1	–	−0.301	Ex	2	1
Aricia agestis	32	35	+0.038	Vu	3	1
Polyommatus semiargus	24	1	−1.097 (−−−)	CE	3	1
Polyommatus icarus	130	128	−0.007	S/LR	3	1
Argynnis paphia[(w)]	19	11	−0.222	CE	3	2
Argynnis aglaja[(w)]	14	3	−0.574 (−)	Ex	2	1
Argynnis adippe	5	–	−0.845	Ex	3	2
Argynnis niobe	4	–	−0.699	Ex	2	1
Issoria lathonia[(w)]	37	6	−0.735 (−−−)	CE	4	1
Boloria euphrosyne	10	–	−1.041 (−−)	Ex	2	1
Boloria selene	27	–	−1.447 (−−−)	CE (Ex)	2	1
Inachis io	150	150	0	S/LR	4	3
Aglais urticae	150	150	0	S/LR	4	3
Polygonia c-album	128	141	+0.042 (+)	S/LR	4	3
Araschnia levana	128	138	+0.032	S/LR	4	3
Nymphalis antiopa[(w)]	18	10	−0.237	Ex	4	3
Nymphalis polychloros[(w)]	40	21	−0.270 (−−)	En	4	3
Euphydryas aurinia	12	–	−1.114 (−−−)	Ex	1	1
Melitaea cinxia	21	1	−1.041 (−−−)	CE	2	1

(*continued on next page*)

Appendix (*cont.*)

Melitaea diamina	3	–	−0.602	Ex	1	2
Melitaea athalia	10	–	−1.041 (−−)	Ex	2	1
Limenitis camilla	26	16	−0.201	Vu	2	2
Apatura iris	9	5	−0.222	En	2	3
Pararge aegeria	150	150	0	S/LR	3	2
Lasiommata megera	127	100	−0.103 (−−−)	S/LR	3	2
Coenonympha tullia	6	–	−0.845 (−)	CE (Ex)	1	1
Coenonympha pamphilus	128	94	−0.133 (−−−)	S/LR	2	1
Pyronia tithonus	87	105	+0.081 (+)	S/LR	2	2
Aphantopus hyperantus	78	68	−0.059	S/LR	2	2
Maniola jurtina	121	127	+0.021	S/LR	3	2
Hipparchia semele	47	19	−0.380 (−−−)	Vu	3	1
Species at the edge of their distribution area in Flanders (not used in the analysis)						
Pyrgus armoricanus	2	–	−0.477	Ex	2	1
Heteropterus morpheus	1	1	0	R	1	2
Cupido minimus[(w)]	2	1	−0.176	R	1	1
Limenitis populi	3	–	−0.602	Ex	2	2
Coenonympha hero	3	–	−0.602	Ex	1	2
Melanargia galathea[(w)]	4	7	+0.204	R	2	1
Hipparchia statilinus	3	–	−0.778	Ex	2	1

[a] Some of the squares may be observations of wanderers; Trend, Log_{10} (number of squares since 1991+1) − Log_{10} (number of squares before 1991+1); significant decreasing/increasing trends are indicated by −−− (Fisher exact two-tailed $P<0.001$); −− (Fisher exact two-tailed $P<0.01$); −/+ (Fisher exact two-tailed $P<0.05$); RLC, Red List category: Ex, Extinct in Flanders; CE, Critically endangered; CE (Ex), categorised as Critically endangered but extinct in the meantime; En, Endagered; Vu, Vulnerable; IK, Insufficiently known; R, Rare; S/LR, Safe/Low risk. Mobility class (based on Bink, 1992): 1, very sedentary, 2, sedentary, 3, fairly sedentary, 4, mobile-very mobile. Nutritional value of the breeding habitat (based on the average nutrient number of the hostplant(s) according to Ellenberg et al., 1992): 1, oligotrophic; 2, mesotrophic; 3, eutrophic.

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